

REVISION OF THE WORLD SPECIES
OF *APLYSIA*
(GASTROPODA, OPISTHOBRANCHIA)

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Aplysia dactylomela. From a painting of the living animal made in 1841 by Dr. J. Stuart and reproduced by Hutton, 1923, labelled *Tethys angasi* Sowerby. The rings on the skin are irregular in size and thickness, and are linked by fine reticulations; they have light centres. The edges of the parapodia are pale and fimbriated, inside they are barred with vertical black bands. Posteriorly the parapodia unite low down, level with the floor of the mantle cavity, fully exposing the large, broad, fluted anal siphon. $\times \frac{1}{2}$.

[Frontispiece]

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SYNOPSIS

A review of the genus *Aplysia* and of the geographical distribution of its members has been made, based on the collections of the British Museum (Natural History) with comparative material from other national museums of Natural History, Marine Biological Stations and private collectors all over the world. The genus can be divided into five subgenera: *Pruvotaplysia*, the most primitive, with two species; *Neaplysia*, North American, with probably only one species; *Varria* nov., with more than twenty species; *Aplysia*, with six species; and *Phycophila*, of the Pacific, with one, possibly two species.

Full descriptions of the species are given, and the following new species are described: *cronullae*, *dura*, *gracilis*, *rehderi*, *reticulata*, as well as a new variety, *delli* of *A. nigra*. Their affinities with one another and with other subfamilies of the Aplysiidae are discussed.

I. INTRODUCTION

(a) *Definition of the Subfamily and Genus*

THE Tectibranch family Aplysiidae contains four subfamilies:

Aplysiinae: *Syphonota* and *Aplysia*.

Dolabellinae: *Dolabella*.

Dolabriferinae: *Dolabrifera*, *Petalifera*, *Phyllaplysia*.

Notarchinae: *Notarchus*, *Stylocheilus*, *Barnardaclesia*, *Bursatella*.

The Aplysiinae are mostly large molluscs, with humped body, the skin usually with reticulate black markings, but without warts or villi. There are no separate oral lobes. The cephalic tentacles are broad and folded, the rhinophores slit like hare's ears. The foot has a short or moderately elongated tail. The parapodia are well developed, symmetrical, mobile, upstanding, separated anteriorly, free or joined posteriorly, typically natatory. The mantle encloses the shell, with or without a mantle foramen. Sub-pallial glands secrete either a purple or a white fluid. The anal siphon is usually tubular and erect, the opaline gland simple or compound. The genital aperture is inside the dorsal slit, anterior to the ctenidium. Shell narrow to broad, flexible, with reduced calcareous layer and apex, with an anal sinus on the right posterior border. Jaws large, radula with wide, denticulate rhachidian tooth and bi-serrate laterals. Caecum with a typhlosole present. Penis unarmed, penis sheath rarely armed, no penial collar. Nerve ring with three pairs of ganglia, pleurovisceral cords long, supra-intestinal and visceral ganglia adjacent, forming a pair or fused. There are two genera, *Syphonota* and *Aplysia*.

SYPHONOTA Adams, 1854¹

Head broad, with rhinophores set close together and far back between the anterior ends of the parapodia. Foot broad. Parapodia free posteriorly, the backwardly directed anal siphon projecting through the gap between them, the shell and mantle tilted towards the animal's left side. Purple glands present. Opaline gland simple, multiporous. Genital aperture almost mid-dorsal, not covered by the mantle flap. Caecum not reaching the surface of the digestive gland.

Type species *Siphonotus geographica* Adams & Reeve, 1850. Circumtropical. Probably only one species. Baba (1955, pl. 1) gave a good coloured figure of this species.

APLYSIA L., 1767

Body soft in most species, elongated but strongly contractile, assuming the "sitting hare" position. The head is more shapely than in *Syphonota*, with erect rhinophores not far distant from the cephalic tentacles, so that a neck region is present between the head and the parapodial attachment. The foot varies from narrow to medium or broad, with a relatively short tail. The upstanding parapodia are mobile and usually natatory, joined high up in some species, shutting in the mantle cavity posteriorly; meeting or joining low down on the foot in others, so that the mantle cavity, as in *Syphonota*, is open at both ends. Anal siphon erect. Secretion from the mantle glands purple except in the subgenus *Aplysia* where it is white or black. Opaline gland simple or compound, multiporous or uniporous respectively. Penis varying from short and broad to long and filiform, penis sheath smooth distally except in subgen. *Aplysia* where it is lined with warts bearing spines. Shell ovate or rounded, horny, with an imperfect calcareous lining; in the subgenus *Neaplysia* the apex of the shell is flattened and rectangular, in all others recurved or hooked. Radula large, multiserial, all the teeth denticulate in most species

¹ To replace *Siphonotus* Adams & Reeve, 1850 (*nec* Brandt, 1837).

except for a few vestigial teeth at the end of the row. Caecum appearing on the surface of the digestive gland. Cerebral ganglia distinct or fused. Parietal (supra-intestinal) and visceral ganglia free or fused.

Numerous species, most of which are tropical ; others live in the temperate zone up to high latitudes.

Type species *A. depilans* Gmelin. European.

(b) Subgenera

The genus *Aplysia* can be divided into five subgenera :

1. *Pruvotaplysia* Engel, 1936, type *Aplysia parvula* Guilding in Mörch, 1863, a primitive subgenus with two species.

2. *Neaplysia* Cooper, 1863, type and only species *A. (N.) californica* Cooper.

3. *Varria*¹ nov., type *Aplysia dactylomela* Rang, 1828. Twenty-five species are here recognized.

4. *Aplysia* Linnaeus, 1767 (as *Laplysia*, probably a printer's error), type *A. depilans* Gmelin, 1791². Six species, on one of which, *A. juliana* Quoy & Gaimard, was founded the subgenus *Tullia* by Mme. Pruvot-Fol, who did not realize that its peculiarities were shared by the type species of the genus.

5. *Phycophila* A. Adams, 1861, type *Placobranchus euchlora* M. E. Gray, 1850 (ex Adams unpublished). This subgenus includes oceanic floating Aplysias known in the Pacific Ocean and belonging to one or possibly two species.

Characters of the Subgenera

1. *Pruvotaplysia*. The foot is narrow, with a pointed tail ; the parapodia are joined high up posteriorly, closing in the mantle cavity behind. There is a flat, unrayed mantle aperture over the strongly concave shell, which usually has remnants of a spiral at its apex. The mantle glands secrete purple, the opaline gland is simple and multiporous, the radula small, with not more than 40 rows and fewer than 25 laterals on each side in a row. The ganglia of the nerve ring and of the visceral group (supra-intestinal and infra-intestinal plus visceral) are rounded and distinct. All these features can be regarded as primitive. There are two species, *parvula* the type and *punctata*, the former circumtropical, the latter in the north temperate and arctic Atlantic areas of the Old World.

2. *Neaplysia*, with one species, *californica*. Giant forms, with strongly mottled skin. Foot broad, but with a long slender tail. Parapodia joined posteriorly low down. Mantle aperture minute or closed. Purple secretion from the mantle glands. Opaline gland large, compound, uniporous. The only peculiarity of this subgenus is the shell, which has a flattened calcareous apex, instead of a reduced spiral or hook. This rectangular flattening was described by Cooper (1863) as an accessory plate, but is part of the shell itself. In all other features the affinities are with subgenus *Varria*. The species is confined to the eastern North Pacific area.

3. *Varria*. This group contains about seven-tenths of the known species, which

¹ *Varria* from Varro, the name of a famous Roman scholar and writer.

² Opinion 200 of the International Commission on Zoological Nomenclature. See p. 396.

show remarkable generalization of structure, despite a great range of size. The parapodia are joined low down posteriorly, exposing the mantle cavity to a through current, since it is open at both ends, and although the anal spout is typically erect, it can be directed backwards between the parapodia as in *Syphonota*. In a few species, e.g. *inca*, *rehderi*, preserved specimens exhibit a low wall not more than 10 mm. high posteriorly, but in the living animal this probably forms a flat extension of the mantle floor, as it does in other species. It is quite unlike the high fusion in the subgenera *Pruvotaplysia* and *Aplysia*. There is always a purple secretion from the mantle glands. About half the members of this group have a simple multiporous opaline gland, the other half a compound uniporous gland, with gradations between them in some species, e.g. *cornigera*, *keraudreni*, *pulmonica*. The foot is narrow in the majority, of medium width in *cervina*, *oculifera* and *winneba*, and broad in *dactylomela*, *denisoni*, *gigantea*, *keraudreni* and *pulmonica*. The penis is filiform in *cronullae*, *fasciata*, *keraudreni*, *kurodai*, *sowerbyi*, *sydneyensis*, *willcoxi* and *winneba*, broad and spatulate in *dactylomela*, *denisoni*, *gigantea* and *pulmonica*, but tapering in the remaining species. The shell varies, but it never possesses a flat, plate-like apex, and is usually rather shallow. The radula is well developed, with many rows (up to about 80) and numerous laterals (to approximately 60); the laterals are multidenticulate except in *dactylomela* and *pulmonica*, where the denticulations exhibit feeble development in young teeth but disappear later, producing long, smooth-edged cusps, usually with a single stout lateral denticle. The caecum is straight or only slightly bent at the tip. The nerve ganglia exhibit fusion of the cerebral and of the visceral pair, except in *sagamiana*, which has small rounded discrete ganglia as in *Pruvotaplysia*. In its small size, simple multiporous opaline gland and narrow foot, *sagamiana* resembles *parvula*, but in its small rayed mantle aperture, rather flat shell without spiral apex and low junction of the parapodia posteriorly its affinities are with *Varria*. The distribution is in all oceans except the Arctic and Antarctic regions. Type *A. dactylomela*.

4. The subgenus *Aplysia* includes the type species of the genus, *A. depilans*. The body is low and flat, bulky, with a broad head. There is a broad foot, capable in most species of producing posteriorly a rounded but temporary sucker. The rather small parapodia are joined high up posteriorly. There is a flat mantle aperture. Purple is not secreted, but both the mantle glands and the simple, multiporous opaline gland secrete a white fluid, rarely a black, which is copious and odoriferous in the case of the opaline gland. The radular teeth are simple, but the number of rows and of teeth in a row reaches the maximum for the genus. The salivary glands are broad and flat, the caecum spiral at the tip. The penis is stout, heavily pigmented, and lies in a sheath which is armed with spiny warts. Six species are known. Distribution circumglobal in tropics and sub-tropics.

5. *Phycophila*. This includes small floating species, about which little is known. Only one species, *euchlora*, from the western Pacific area, has been described. The cephalic tentacles are broad, curved and pointed, the body slender, with a narrow foot and long, tapering tail. The parapodia are freely mobile and meet low down on the tail. The mantle is small, the shell sac closed. The opaline gland is small, simple and multiporous. The penis is filiform.

List of Recognized Species of Aplysia

	Page	Subgenus <i>Varria</i> (cont.):	Page
Subgenus <i>Pruvotaplysia</i> :		<i>morio</i>	328
<i>parvula</i>	287	<i>oculifera</i>	332
<i>punctata</i>	291	<i>pulmonica</i>	335
		<i>rehderi</i>	337
Subgenus <i>Neaplysia</i> :		<i>reticulata</i>	340
<i>californica</i>	294	<i>robertsi</i>	342
		<i>sagamiana</i>	343
Subgenus <i>Varria</i> :		<i>sowerbyi</i>	345
<i>brasiliانا</i>	297	<i>sydneyensis</i>	348
<i>cervina</i>	299	<i>willcoxi</i>	350
<i>cornigera</i>	302	<i>winneba</i>	352
<i>cronullae</i>	304		
<i>dactylomela</i>	307	Subgenus <i>Aplysia</i> :	
<i>denisoni</i>	310	<i>cedrosensis</i>	354
<i>extraordinaria</i>	312	<i>depilans</i>	357
<i>fasciata</i>	315	<i>dura</i>	360
<i>gigantea</i>	318	<i>juliana</i>	363
<i>gracilis</i>	320	<i>nigra</i>	369
<i>inca</i>	321	<i>vaccaria</i>	371
<i>keraudreni</i>	322		
<i>kurodai</i>	325	Subgenus <i>Phycophila</i> :	
<i>maculata</i>	326	<i>euchlora</i>	374

Rejected Names

Names considered invalid or of doubtful validity because of inadequate description and absence of a specimen. It is possible that some of these are synonyms of known species, but there is not sufficient information to establish their identity.

- adamsi* Pilsbry, 1896 : 112. Borneo.
chierchiana Mazzarelli & Zuccardi, 1892 : 13. Peru.
fusca Tilesius, 1809-13 : China and Japan.
laevigata Stimpson, 1855 : 378. China.
marginata and *marmorea* A. Adams, 1861 : 140. China.
punctatella Bergh, 1902 : 341. Philippines.
sinensis Sowerby, 1869 : China.
spuria Krauss, 1848 : 71. South Africa.
tarda Verrill, 1901 : 26. Bermuda.
tryonii Meinertzhagen, 1880 : 270. New Zealand.
venosa Hutton, 1875 : 279. New Zealand.
vexans Bergh, 1905 : 10. Amboina, East Indies.
Siphonota elongata Pease, 1860 : 24. Hawaii.
Siphonota grandis Pease, 1860 : 23. Hawaii.

Names given to juvenile forms whose status is doubtful :

- parva* Pruvot-Fol, 1953 : 38. Morocco. According to Marcus, 1958 : 10 this is a young *juliana*.

sorex Rang, 1828 : 57 (see p. 363).

Esmia griffithsiana Leach, 1847 : 268 (see p. 292).

vistosa Pruvot-Fol, 1953 : 37. Morocco.

Species named from shells only and unidentifiable from the descriptions : *bipartita*, *elegans* and *macula* Turton, 1932 : South Africa.

Name given to a probable hybrid :

Siphonota lobiancoi Mazzarelli, 1890 : 42 (p. 315).

(c) *History of the Genus*

Aplysia has been known from ancient times, the first authentic description being that of Pliny in the first century, A.D. He called it *Lepus marinus*, the Sea Hare, and described three kinds, two in the Mediterranean, and one, probably a *Dolabella*, in the Indian Ocean. He gave an account of the supposed poisonous qualities of this harmless mollusc. Other early writers compared it with a snail (Aelian) or a cuttlefish (Dioscorides).

In 1554 Rondelet included three kinds of *Lepus marinus* among the fishes in his *De Piscibus Marinis*, the first of which we now know as the Nudibranch *Tethys leporina*. He explained that it should not be confused with other fishes because "it is very poisonous and would be fatal to anyone who ate it". But Gesner in 1551 had recognized that it was not a fish and placed it among the soft-bodied animals.

Redi in 1684 called it the Sea Slug and described its internal anatomy, and a century afterwards Bohadsch, a Bohemian fugitive living in Naples, published in 1761 a book on marine animals, describing two kinds under the name of *Lernaea*. He studied their habits and observed the discharge of purple and milk-white secretions. The opaline gland is sometimes called by his name. He realized that his *Lernaea* is related to the land snail.

British observers in the eighteenth century classified *Aplysia* amongst the Holothurians (Borlase, 1758) and the worms (Pennant, 1777).

In 1756 Linnaeus, in the 9th edition of the *Systema Naturae*, used *Lerneæ* (later adopted by Bohadsch as *Lernaea*) for the Sea Hare; in the 10th edition (1758) he changed it to *Tethys*, mentioning two species, which he called *T. limacina*, with the habitat "Oceano Australi" and *T. leporina* (= *Lepus marinus*) in the Mediterranean; in the 12th edition, 1767 he changed the diagnosis, applied the name *Tethys* to the animal we know now as a Nudibranch and called the Sea Hare *Laplysia* (probably a printer's error), choosing as the type *L. depilans*¹; finally in the 13th edition (1791) Gmelin corrected the spelling to *Aplysia*.

¹ The word *Aplysia* means "that which one cannot wash" and was used by Aristotle for a sponge which could not be freed from grit and sand. Linnaeus chose the name arbitrarily. *Aplysia* came into common usage for the Tectibranch, *Tethys* for the Nudibranch. On the question of priority Pilsbry changed *Aplysia* to *Tethys*, thus making *Tethys* a genus of the family Aplysiidae and *Aplysia* a genus of the family Tethyidae. The International Commission on Zoological Nomenclature (Op. 200, 1954, 3, 239-266) decided that the name *Aplysia* should be validated for the Tectibranch notwithstanding the Linnaean name in the 10th edition.

In the nineteenth century Lamarck (1822) classified the Aplysiidae near the Bulliidae. Cuvier in 1803 published a memoir on the genus "*Laplysia*" and gave the first full account of its anatomy, with good figures. European and especially Mediterranean species occupied the attention of Risso (1818), delle Chiaje (1828), de Blainville (1823), Milne Edwards (1847), Vayssière (1885) and Mazzarelli (1893), while the great voyages of the period brought specimens from foreign coasts in all parts of the world. Rang's monograph *Histoire naturelle des Aplysiens*, 1828 is still valuable for the descriptions and figures it contains. He accounts for 22 species of the genus *Aplysia*, which the modern systematist would reduce to seven or eight. He knew the three Mediterranean species *punctata*, *depilans* and *fasciata*, but did not realize that some species are circumtropical. In fact, this has always caused confusion in the genus. Local names have been given to world-wide species, thus multiplying the number of synonyms. Rang's species are *brasiliانا*, *dactylomela*, *maculata*, *keraudreni*, *depilans*, *fasciata* and *punctata*.

At the end of the century the great monograph of Tryon appeared, Pilsbry contributing the section on the Aplysiidae, published in 1895 and 1896. Although largely a compilation from many authors it is the most comprehensive work existing on the family. He records at least 20 authentic species under the name *Tethys*, with numerous synonyms.

The expansion of our knowledge in the nineteenth and twentieth centuries is due to two groups of workers. The marine expeditions collected material from all the oceans, depositing it in the National Museums of the countries concerned. In some cases it was investigated, but often it was left unnamed. Some of these collections have been used by the author and provide interesting finds. For example, specimens of *Aplysia extraordinaria* from New South Wales, a species named by Miss Allan in 1932, have been in the Paris National Museum since 1874 and in the British Museum (Natural History) since 1883. *Aplysia morio*, described by Verrill from Bermudan examples in 1901, has been represented by a good specimen in the Swedish national museum since 1889.

The other group of workers consists of the local collectors who name their own species, often without access to known species for comparison, or to the literature. Frequently they failed to recognize world-wide species, with the result that synonyms were multiplied, young individuals were sometimes given specific rank and imperfect descriptions may make the species unrecognizable. Still more reprehensible was the naming of species from the dried shell alone, for shell shape is one of the most variable characters in the genus. To all who undertake to name new species, the author would recommend a study of p. 277 which gives the characters necessary for the identification of a species of *Aplysia*.

The seas of the world may be divided into ten areas according to the distribution of species of *Aplysia* (see Geographical Distribution, p. 377). This division is convenient but not arbitrary. Each area has been investigated by one or both of the two groups of zoologists mentioned above.

The three European species *punctata*, *fasciata* and *depilans* are perhaps best known, although synonyms are numerous. Work on them during the nineteenth century was initiated by Cuvier (1803 and 1817), continued by the compilations of